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Research article

Genetic analysis for forage yield and quality characters in cowpea (Vigna unguiculata L. Walp)

Manmeet Singh Dhillon, Devinder Pal Singh* and Meenakshi Goyal

Punjab Agricultural University, Ludhiana-141004, India *Corresponding author email: devinderpal301@pau.edu

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Abstract

This study was carried out to determine the combining ability of forage yield, its components and quality traits among crosses derived from nine selected cowpea parents. About 36 crosses were generated from diallel crosses, excluding reciprocals. These crosses and nine parents were evaluated for combining ability for forage yield, its components and quality traits. The results indicated that parent 85-5E was the best combiner for green fodder yield, dry matter yield, leaf length, leaf breadth, number of leaves per plant, number of branches per plant, crude protein content and *in-vitro* dry matter digestibility. Similarly, parent FOS 1 proved to be the best combiner for vine length, number of leaves per plant, number of branches per plant, crude protein content and *in-vitro* dry matter digestibility. The crosses involving FOS 1 x CL 398, CL 391 x C 88, FOS 1 x C 74, CL 396 x CL 391 and FOS 1 x C 88 were the best specific combiner for green fodder yield and most of its components traits. The ratio of *gcalsca* values was greater than unity for most of the forage and quality traits, inferring that additive gene action played an important role in their inheritance. In contrast, for traits like vine length, dry matter yield, crude protein content, and *in-vitro* dry matter digestibility, the above-said ratio was less than unity, indicating non-additive gene action played an important role. So, to utilize both additive and non-additive gene effects, modification of conventional breeding methods such as bi-parental breeding or reciprocal recurrent selection will be the better choice for initiating any cowpea breeding program.

Keywords: Combining ability, Cowpea, Forage yield, Quality characters

Introduction

Cowpea [Vigna unguiculata (L.) Walp.] is a highly nutritious legume crop grown in arid and semi-arid regions of Africa, Asia, Central and South America. Cowpea in India is grown for green pods, vegetables, dry seeds, green manure and forage. Cowpea improves soil fertility and soil health. Cowpea can be cultivated in both summer and kharif seasons. In Punjab, cowpea is mainly grown as a fodder crop from March to July. It supplies nutritious and palatable fodder during summer when green fodder is scarce.

In the current scenario of the changing environment, more nutritious, disease-resistant and high-yielding fodder varieties are needed. The forage yield, being quantitative and polygenic, depends on many independent component traits. Hence, the knowledge regarding the genetic structure of important yield components forms the basis for suitable breeding methodology. The ability of parents to combine well is controlled by complex

interactions among the genes, which cannot be judged only by the yield performance of parents and their hybrids. Hence, combining ability analysis helps select desirable parents and provides information regarding the nature and magnitude of gene effects controlling critical quantitative traits. Jinks and Hayman (1953) made crosses among homozygous parents in a diallel fashion to obtain information regarding combining ability and nature of gene action involved. As per their study, combining ability depicts the breeding value of parental lines to produce hybrids. A high general combining ability value of parents indicates a more significant role of additive variance, while a higher specific combining ability value predicts the dominance gene effect.

The present investigation was conducted on two generations, (i) parents and (ii) F1s developed from diallel crosses among these parents. The evaluation of parents and their hybrids was done on the basis of their combining ability. The effect of gene interaction on

forage yield and quality traits was studied. Combining ability analysis and study of the nature of gene action would help cowpea breeders identify superior parents and breeding methodologies successfully and select promising genotypes from the segregating populations to improve forage and quality traits in cowpeas.

Materials and Methods

Study site and design: The proposed research was conducted in an experimental area of the Forage, Millet and Nutrition Section of the Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana. The nine morphological distinct lines of cowpea *viz.*, CL 367, 85 -5E, CL 396, C 74, BCM 8, C 88, CL 398, FOS I and CL 391 and their 36 crosses obtained from 9 x 9 diallel cross without reciprocals were sown during *kharif* 2022. The material was sown in a randomized complete block design, and data was replicated thrice. Each entry was sown in two rows of 5 m in length with row-to-row and plant-to-plant spacing of 60 cm and 30 cm, respectively. The non-experimental rows were planted around experimental rows to avoid border row effects. All the recommended agronomic and plant protection measures were carried out to raise a good crop.

Observations recorded and genetic analysis: The observations were recorded for fourteen attributes, viz., vine length, stem girth, leaf: stem ratio, leaf length, leaf breadth, number of leaves per plant, number of branches per plant, days to flowering, green fodder yield, dry matter yield, crude protein content (CP), in-vitro dry matter digestibility (IVDMD), acid detergent fiber (ADF) and neutral detergent fiber (NDF). The observations on five random competitive plants of each genotype were made in each replication before harvesting the fodder crop (60 days after sowing). The genetic analysis was conducted using the second method suggested by Griffing (1956).

Results and Discussion

Analysis of variance: The analysis of variance showed significant differences among the genotypes for all the characters. The partitioning of genotypic variance into parents, hybrids and parents v/s hybrids revealed significant differences for almost all important traits (Table 1). The analysis of variance for the combining ability for forage yield and other traits was significant for all the characters under study. This indicated the presence of additive gene effects for all the traits related to green fodder yield and quality in forage cowpeas. The ratio of gca/sca values was greater than unity for stem girth, leaf: stem ratio, leaf length, leaf breadth, number of leaves per plant, number of branches per plant, days to flowering,

green fodder yield, acid detergent fiber and neutral detergent fiber inferring that additive gene action played an important role in their inheritance (Table 1). Dinkar *et al.* (2018) also reported a preponderance of additive gene action for most of these forage and quality traits. But Bhardwaj *et al.* (2023) revealed that additive gene action predominated in the inheritance of forage yield traits, whereas non-additive gene action was predominant for forage quality traits.

Estimates of general combining ability effects: The general combining ability effects results depicted that parent 85-5E was the best combiner for green fodder yield, dry matter yield, leaf length, leaf breadth, number of leaves per plant, number of branches per plant, crude protein content and in-vitro dry matter digestibility, which might be due to favorable genes present for these traits (Table 2). Parent C 88 exhibited the highest positive significant gca effect and was an excellent combiner for earliness. Both parents (C 88 and 85-5E) also depicted a positive significant *gca* effect for leaf length and breadth. Another parent, FOS 1, also proved to be the best combiner for vine length, number of leaves per plant, number of branches per plant, crude protein content and *in-vitro* dry matter digestibility. Among the quality traits, parent C 88 was the best general combiner for decreased acid detergent fiber and neutral detergent fiber as it had a maximum negative significant gca effect for both traits. No single parent was superior to all the characters for the general combining ability values. Parents' gca and per se performance need to be analyzed because superior combiners for different characters will produce desired segregants (Singh and Singh, 1985; Pethe et al., 2018).

Estimates of specific combining ability effects: The analysis of variance for specific combining ability was also found to be either significant or highly significant for all the traits, which showed that dominance gene effects were also involved (Table 3). The cross involving FOS 1 x CL 398 was the best specific combiner for green fodder yield, followed by CL 391 x C 88, FOS 1 x C 74, CL 396 x CL 391 and FOS 1 x C 88. For dry matter yield, CL 391 x C 88, which was medium x medium based on the gca effect, was a superior specific combiner, followed by FOS 1 x CL 398, C 74 x CL 391 and C 74 x C 88. The highest significant positive *sca* effect for vine length was observed for BCM 8 x C 74. The cross CL 398 x CL 391 depicted the highest positive significant sca effect for earliness. The poor x good general combiner involving cross BCM 8 x CL 398 were superior for leaf length and leaf breadth for *sca* effects. For the number of leaves per plant and number of branches per plant, CL 396 x CL 398 was superior. The cross combinations CL 398 x CL 391 and CL 396 x CL 367 were the best specific combiners for quality traits (Table 4).

 Table 1. Analysis of variance for forage and quality traits in cowpea

| | | |) | • | | • | | | | | | | | | | |
|--|-------------------------|----------------|--------|------------------------|----------------|-----------------|----------------------------------|---------------------------------------|----------------------|-----------------------------------|---------------------------------|-------------------------------------|---|-------------------------------------|-------------------------------------|---|
| Source of Degree of | Degree of freedom | Vine length | Stem | Leaf: stem ratio | Leaf length | Leaf breadth | Number of leaves per plant | Number of branches per plant | Days to flowering | Green fodder yield/ plot | Dry matter yield/ plot | Crude protein content (CP) | In-vitro dry matter digestibility (IVDMD) | Acid detergent fibre (ADF) | Neutral detergent fibre (NDF) | |
| Replication 2 | 2 | 97.20 | 0.01 | 0.02* | 0.84 | 0.32 | 4660.10 | 2.95* | 4.80 | 5.52** | 0.12** | 0.03* | 0.26** | 0.04* | 0.01 | |
| Genotypes | 4 | 301.50** | 0.06** | 0.03** | 6.70** | 3.56** | 6490.20** | 3.48** | **06.76 | 3.82** | 0.06** | 6.75** | 50.74** | 18.36** | 20.67** | |
| Parents | 8 | 516.36** | 0.03** | 0.01** | 11.40** | **02.9 | 4350.20** | 4.80** | **06.79 | 1.52 | 0.03 | 4.51** | 36.60** | 18.42** | 51.89** | |
| Hybrids | 35 | 233.68** | 0.08** | 0.03** | 5.45** | 2.98** | 7086.60** | 3.26** | 105.56** | 4.12** | 0.06** | 7.25** | 52.66** | 17.01** | **80.6 | |
| Parents v/s hybrids | 1 | 949.65** | 0.01 | 0.20** | 15.35** | 1.45** | 2601.20 | 1.26 | 46.20** | 16.45** | 0.10* | 10.02** | 97.27** | 64.23** | 177.23** | |
| Error | 88 | 38.40 | 0.01 | 0.00 | 0.45 | 0.31 | 1174.90 | 0.87 | 4.29 | 92.0 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | |
| 8ca | 8 | 72.41** | 0.05** | 0.03** | 6.39** | 2.38** | 3007.65** | 1.76** | 54.60** | 1.37** | 600.0 | 1.17** | 16.34** | 7.31** | 12.71** | |
| sca | 36 | 106.89** | 0.01** | 0.004** | 1.65** | 0.93** | 1971.89** | 1.05** | 27.76** | 1.25** | 0.02** | 2.49** | 17.02** | 5.82** | 5.58** | |
| Error | 88 | 12.76 | 0.003 | 0.001 | 0.16 | 0.10 | 393.65 | 0.29 | 1.43 | 0.26 | 0.005 | 0.002 | 0.004 | 0.004 | 0.004 | |
| 8ca/sca | | 29.0 | 52 | 7.5 | 4.81 | 2.58 | 1.52 | 1.63 | 1.95 | 1.09 | 0.45 | 0.47 | 96:0 | 1.25 | 2.27 | |
| | | | | | | | | | | | | | | | | • |

 $^*(P<0.05); ^{**}(P<0.01);$ gca: General combining ability; sca: Specific combining ability

 Table 2. General combining ability effects of parents for different fodder traits in cowpea

| Parents | Vine length | Stem | Leaf: stem ratio | Leaf length | Leaf breadth | Number of leaves per plant | Number of branches per plant | Days to flowering | Green fodder yield/ plot | Dry matter yield/ plot | Crude protein content (CP) | In-vitro dry matter digestibility (IVDMD) | Acid detergent fibre (ADF) | Neutral detergent fibre (NDF) |
|-----------------------|----------------|---------|------------------------|----------------|-----------------|----------------------------------|---------------------------------------|----------------------|-----------------------------------|------------------------------|-------------------------------------|---|----------------------------------|-------------------------------------|
| CF 367 | 0.52 | 0.00 | -0.02** | 0.13 | 0.11 | -9.52 | -0.43** | -0.40 | -0.02 | 0.00 | 0.09** | -0.18** | -0.77** | -0.71** |
| 85 5E | -2.90** | 0.10** | 0.04** | 0.51** | 0.47** | 7.44 | 0.48** | 1.41** | 0.37* | 0.06** | 0.30** | 1.07** | -0.57** | 0.02 |
| CL 396 | 2.89** | -0.14** | -0.06** | -0.76** | -0.51** | -1.83 | 0.14 | -3.73** | -0.36* | -0.02 | -0.23** | -0.40** | 0.43** | -0.36** |
| C 74 | 1.16 | 0.02 | 0.00 | 0.02 | 0.01 | -3.46 | -0.27 | -0.67 | 0.22 | 0.02 | 0.01 | 0.57** | -0.18** | -0.32** |
| BCM8 | 2.58* | -0.03* | -0.06** | -0.78** | -0.32** | -12.96* | -0.01 | -2.09** | -0.68** | -0.02 | -0.63** | -1.92** | 1.47** | 2.53** |
| C 88 | -3.74** | -0.02 | -0.00 | 0.76** | 0.41** | -9.52 | -0.42** | 4.14** | 0.12 | -0.03 | 0.22 | 0.31** | 1.05** | -0.84** |
| CL 398 | 2.21* | 0.04** | 0.05** | 0.67** | 0.23** | 10.43 | -0.07 | 0.38 | -0.20 | -0.02 | -0.23** | -1.78** | 0.62** | 0.37** |
| FOS I | 2.91** | 0.02 | 0.08** | -1.27** | -0.85** | 31.16** | 0.74** | -0.31 | 0.23 | -0.00 | 0.40** | 1.52** | -0.78** | -0.95** |
| CL 391 | 0.14 | 0.02 | -0.04** | 0.71** | 0.45** | 6.03 | -0.23 | 1.27** | 0.31* | 0.00 | -0.02** | 0.03 | 0.61** | 0.39** |
| SE | 1.01 | 0.02 | 0.01 | 0.10 | 0.09 | 5.66 | 0.16 | 0.33 | 0.14 | 0.02 | 0.01 | 0.02 | 0.02 | 0.02 |
| CD (P<0.05) | 2.01 | 0.03 | 0.02 | 0.21 | 0.17 | 11.28 | 0.31 | 99.0 | 0.28 | 0.04 | 0.02 | 0.04 | 0.04 | 0.04 |
| CD (P<0.01) | 2.64 | 0.04 | 0.02 | 0.20 | 0.25 | 14.68 | 0.40 | 0.90 | 0.38 | 0.05 | 0.03 | 0.04 | 0.04 | 0.05 |
| *(P<0.05); **(P<0.01) | <0.01) | | | | | | | | | | | | | |

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|-----------|--|-------------|------------|---------------------|----------------|-----------------|---------------------------|-----------------------------|----------------------|----------------------------|
| S. No. | Crosses | Vine length | Stem girth | Leaf: stem ratio | Leaf length | Leaf breadth | Number of leaves/plant | Number of branches/plant | Days to flowering | Green fodder yield/plot |
| 1 | BCM 8 x CL 396 | 12.76** | 0.12** | 0.02 | -0.85** | -0.96** | 12.97 | -0.78 | 7.12** | 0.41 |
| 2 | $BCM~8\times FOS~1$ | 0.29 | -0.01 | -0.006 | -1.49** | -0.99** | 55.01** | 1.97** | 0.71 | -0.67 |
| 3 | BCM $8 \times 85-5$ E | -4.26 | -0.02 | -0.02 | -0.78* | -0.47 | -12.27 | -0.74 | 3.32** | 1.15** |
| 4 | $BCM 8 \times C 74$ | 24.65** | -0.04 | 0.02 | -0.29 | 0.16 | -16.09 | 0.33 | 3.05** | -0.67 |
| 5 | BCM $8 \times CL 398$ | 9.32** | 0.10* | 0.02 | 1.90** | 1.61** | -14.68 | -0.53 | 1.02 | 0.23 |
| 9 | BCM $8 \times CL 391$ | -0.94 | -0.004 | -0.06* | 1.14** | 1.07** | 25.39 | 1.32** | 0.42 | -0.10 |
| ^ | $BCM 8 \times C 88$ | 6.94* | 0.07 | 0.002 | 1.60** | 1.43** | -6.29 | 0.50 | -5074** | -0.91* |
| 8 | BCM $8 \times CL 367$ | -0.006 | 0.15** | 0.04 | *08.0 | 0.81** | 30.44 | 1.06* | 6.46** | 0.41 |
| 6 | CL396 x FOS 1 | -5.17 | -0.10* | 0.001 | -0.17 | -0.48 | -76.76** | -1.16** | -7.95** | -1.68** |
| 10 | CL396 x 85-5 E | 2.62 | -0.04 | -0.01 | 1.51** | 1.36** | 10.96 | 1.10* | -0.70 | -0.17 |
| 11 | CL396 x C 74 | -7.78** | 0.007 | **60.0- | -0.82* | -0.84** | -28.85 | 0.19 | 5.01** | -0.66 |
| 12 | CL396 x CL 398 | 3.14 | 0.22** | 0.05 | -0.12 | 0.27 | 75.93** | 2.31** | -0.01 | -1.57** |
| 13 | CL396 x CL 391 | -10.09** | -0.22** | 0.08** | -2.03** | -1.42** | -29.66 | -0.16 | -7.59** | 1.56** |
| 14 | CL396 x C 88 | 13.43** | 0.18** | 0.05 | -0.57 | 0.10 | -5.74 | 0.33 | -1.44 | -0.90 |
| 15 | CL396 x CL 367 | -26.15** | -0.004 | 0.02 | -1.77** | -1.76** | -9.99 | -1.42** | -7.21** | 0.55 |
| 16 | FOS 1 \times 85-5 E | -3.21 | -0.01 | 0.07* | -1.27** | -0.47 | -87.38** | -1.83** | -2.44* | -0.08 |
| 17 | $FOS1 \times C74$ | 8.05** | -0.13** | -0.04 | 1.54** | 1.32* | -37.82* | 0.58 | 2.29* | 1.74** |
| 18 | FOS 1 \times CL 398 | -5.01 | -0.15** | 0.02 | -0.44 | 0.42 | 57.23** | -0.61 | -3.41** | 2.14** |
| 19 | FOS 1 \times CL 391 | 5.42 | -0.02 | -0.10** | -0.50 | -0.247 | -33.30* | 0.88* | -3.33** | -0.66 |
| 20 | $FOS1 \times C88$ | 4.29 | 0.22** | -0.04 | 0.77* | -0.07 | 45.32** | -0.26 | 0.16 | 1.17** |
| 21 | FOS 1 \times CL 367 | 2.69 | -0.01 | *90.0 | 1.24** | 1.21** | 2.36 | -0.02 | 4.71** | -1.36** |
| 22 | $85-5 E \times C 74$ | -4.81 | -0.10* | -0.08** | 0.74* | 0.001 | 5.19 | -0.47 | 0.24 | 1.08** |
| 23 | $85-5 \text{ E} \times \text{CL } 398$ | -8.87** | -0.02 | -0.08** | 0.27 | -0.39 | -6.02 | 0.63 | -1.80 | -1.15** |
| 24 | $85-5 \text{ E} \times \text{CL } 391$ | -5.44 | -0.10* | -0.02 | -0.46 | -0.08 | -77.91** | 0.50 | -3.70** | -2.50** |
| 25 | $85-5 E \times C 88$ | -1.91 | 0.004 | **60.0 | 0.32 | 0.10 | 34.99* | 89.0 | -1.88 | -0.13 |
| 26 | $85-5 \text{ E} \times \text{CL } 367$ | 7.47* | -0.12** | 0.0003 | 0.77* | 0.56* | 9.74 | 0.58 | 99.0 | -0.06 |
| 27 | C 74 x CL 398 | -0.28 | 0.12** | 0.004 | .78* | 1.23** | 41.82** | -1.61** | 0.27 | -0.13 |
| 28 | C 74 x CL 391 | -14.19** | 0.10 | 0.04 | 1.02** | 0.71** | 72.61** | 0.57 | -5.65** | 0.32 |
| 29 | C 74 x C 88 | -0.97 | 0.02 | 0.02 | -0.36 | 80.08 | 14.15 | 0.77 | -1.83 | 0.02 |
| | | | | | | | | | | 1 |

Table 3. Specific combining ability effects of crosses for different fodder traits in cowpea

| S. | Crosses | Vine lenoth | Stem oirth | Leaf: stem | Leaf | Leaf | Number of | Number of | Days to | Green fodder |
|--------|---|-------------|------------------|--|--------------------|--------------|----------------------|-------------------------|------------------|---------------------|
| No. | | 9 | | ratio | length | breadth | leaves/plant | branches/plant | flowering | yield/plot |
| 30 | C 74 x CL 367 | 1.08 | 0.02 | 0.02 | -1.06** | -0.96** | 10.24 | 0.34 | -8.62** | -0.84* |
| 31 | CL 398 x CL 391 | 3.07 | -0.01 | -0.008 | 0.05 | -0.52 | -43.24** | *86.0- | 11.99** | 0.57 |
| 32 | CL 398 x C 88 | -11.36** | -0.20** | *90.0 | -0.33 | -0.32 | -61.38** | -0.44 | -7.53** | 0.17 |
| 33 | CL 398 × CL 367 | 0.64 | -0.12** | 0.02 | -0.37 | -1.02** | -6.28 | 0.80 | 1.68 | -0.57 |
| 34 | $CL 391 \times C 88$ | -4.28 | 0.15** | -0.17* | 0.44 | -0.18 | **80.89 | 0.40 | 8.24** | 1.90** |
| 35 | $CL 391 \times CL 367$ | 2.78 | 0.02 | -0.04 | 90.0 | 0.11 | -4.49 | -1.02* | 4.12** | -0.33 |
| 36 | C 88 × CL 367 | -8.67** | -0.22** | -0.17** | -1.98** | -0.85** | -45.62** | -1.15** | 3.27** | -1.23** |
| | SE | 2.88 | 0.04 | 0.03 | 0.32 | 0.26 | 16.05 | 0.44 | 96:0 | 0.41 |
| | CD (P<0.05) | 5.74 | 0.09 | 90.0 | 0.64 | 0.52 | 31.85 | 0.89 | 1.92 | 0.82 |
| | CD (P<0.01) | 7.54 | 0.12 | 0.08 | 0.83 | 99.0 | 41.84 | 1.16 | 2.53 | 1.08 |
| S. No. | S. No. Crosses Dry matter yield/plot Crude prot | Q | Dry matter yield | Id/plot Cruc | Crude protein (CP) | | Acid detergent fibre | Neutral detergent fibre | | In-vitro dry matter |
| - | BCM 8 v CI 396 | | 0.01 | ************************************** | ** | 1 73** | | 4 86** | mgesm -2 84** | Omity (IV Divid) |
| , , | BCM 8 x FOS 1 | | -0.08 | **670- | ** | 1, 30 *TC | | -1 51* | -1 40** | |
| ı m | BCM 8 x 85-5 E | | 0.17** | -1.18** | * | 2.63** | | 2.33** | -2.67** | |
| 4 | BCM 8 x C 74 | | 0.04 | 1.00** | * | -1.44** | * | -3.11** | 3.37** | |
| Ŋ | BCM 8 x CL 398 | | 0.02 | 1.44** | * | -3.96** | * | -4.81** | 3.71** | |
| 9 | BCM 8 x CL 391 | | 0.04 | -1.23** | * | 1.77** | | 4.29** | -3.91** | |
| ^ | BCM 8 x C 88 | | -0.09 | 1.59** | * | -2.78** | * | -3.56** | 3.48** | |
| ∞ | BCM 8 × CL 367 | | 0.04 | 0.92** | * | -0.82** | * | -2.71** | 4.11** | |
| 6 | CL396 x FOS 1 | | -0.03 | 0.91** | * | -3.71** | * | -1.02** | 3.05** | |
| 10 | CL396 x 85-5 E | | 0.00 | 0.32** | * | -0.04 | | -0.52** | 1.35** | |
| 11 | CL396 x C 74 | | -0.06 | -0.42** | * | 1.77** | | 0.80** | -1.90** | |
| 12 | CL396 x CL 398 | | -0.07 | 0.22** | * | 0.08 | | -0.85** | 2.26** | |
| | | | | | | | | | | Cont |

| S. No. | Crosses | Dry matter yield/plot | Crude protein (CP) | Acid detergent fibre (ADF) | Neutral detergent fibre (NDF) | In-vitro dry matter digestibility (IVDMD) |
|-----------------------|--|-----------------------|--------------------|----------------------------|-------------------------------|--|
| 13 | CL396 x CL 391 | 0.08 | -1.07** | 1.16** | 2.14** | -2.41** |
| 14 | CL396 x C 88 | -0.21** | 0.85** | -2.35** | -0.85** | 2.94** |
| 15 | CL396 x CL 367 | -0.07 | 2.47** | -4.21** | -2.10** | 6.23** |
| 16 | FOS 1 x 85-5 E | -0.11* | 0.55** | -0.79** | -1.03** | -0.39** |
| 17 | FOS 1 x C 74 | 0.14** | -0.53** | 2.68** | 1.29** | -2.67** |
| 18 | FOS 1 x CL 398 | 0.17** | -0.10** | 0.59** | 0.77*** | 0.84** |
| 19 | FOS 1 x CL 391 | 0.05 | -0.38** | 1.83** | 0.41** | -2.04** |
| 20 | FOS 1 x C 88 | 0.14** | -0.49** | 1.65** | 1.21** | -0.77** |
| 21 | FOS $1 \times CL$ 367 | -0.10 | **60.0- | 1.42** | 0.73** | 0.67** |
| 22 | 85-5 E x C 74 | 0.004 | *80.0- | 0.77** | -0.40** | 1.01** |
| 23 | 85-5 E x CL 398 | -0.10 | -0.41** | 1.26** | 5.29** | -0.55** |
| 24 | $85-5 \text{ E} \times \text{CL } 391$ | -0.28** | -1.27** | 1.08** | -0.41** | -0.26** |
| 25 | 85-5 E x C 88 | -0.10 | -1.96** | 3.58** | 1.82** | -4.88** |
| 26 | 85-5 E x CL 367 | 0.041 | 1.61** | -2.25** | -1.31** | 1.00** |
| 27 | $C74 \times CL398$ | -0.13* | 0.22** | -0.52** | 0.34** | 0.68** |
| 28 | C 74 x CL 391 | 0.17** | 0.50** | -2.65** | -1.02** | 1.52** |
| 29 | C 74 x C 88 | 0.18** | 0.88** | -1.73** | -0.51** | 2.70** |
| 30 | $C74 \times CL367$ | -0.04 | -2.02** | 4.12** | 2.79** | -6.15** |
| 31 | CL 398 x CL 391 | -0.01 | 5.08** | -1.51** | -3.49** | 9.26** |
| 32 | CL 398 x C 88 | 0.13** | -0.98** | 1.27** | 0.45** | -1.35** |
| 33 | CL 398 x CL 367 | -0.17** | -3.04** | 0.20** | 0.45** | -10.18** |
| 34 | CL 391 x C 88 | 0.22** | -3.06** | 3.42** | 1.61** | **89'6- |
| 35 | CL 391 x CL 367 | -0.12** | 1.48** | -2.68** | -1.67** | 4.67** |
| 36 | C 88 × CL 367 | -0.10 | -0.48** | 1.69** | 1.55** | -1.34** |
| | SE | 90.0 | 0.04 | 0.05 | 0.05 | 0.05 |
| | CD (P<0.05) | 0.11 | 0.07 | 0.10 | 0.10 | 0.10 |
| | CD (P<0.01) | 0.14 | 0.09 | 0.13 | 0.14 | 0.14 |
| *(P<0.05); **(P<0.01) | P<0.01) | | | | | |

The magnitude of variance due to general combining ability was higher than variance due to specific combining ability for all the traits except vine length, dry matter vield, crude protein content, and in-vitro dry matter digestibility. This suggested a greater role of additive gene effects in inheriting various traits. Indeed, the role of the additive gene effect could not be neglected. The results were in close association with earlier research work reported by Sohoo et al. (1987), Jhorar and Jatasra (1990), Madhusudan et al. (1995), Bala et al. (2018) and AL-obeidi et al. (2022). The combining ability effect revealed that parent 85-5E and CL 391 were good general combiners for green fodder and dry matter yield. These parents also produced good hybrids with poor cross-combinations for these traits. The best parents with high gca effect were not always the best specific combiners (Owusu et al., 2018; Singh *et al.*, 2018). The present investigation showed that any single cross was not superior to all the characters studied and was significant to particular characters. The present investigation infers that the superior cross combinations having high sca effects are produced not only when both the parents are good general combiners (high x high) but also when at least one or both the parents are medium or low general combiners. The crosses that were having high *sca* effects from good general combiners (high x high) might be attributed to additive x additive type of gene action and higher yield potential could be fixed in subsequent generations and produce useful transgressive segregants, which could be identified following simple conventional breeding techniques like the pedigree method of selection (Verma et al., 2021). The parents with high x low general combining ability could also produce high *sca* effects owing to additive x epistatic type of gene action. However, the higher yield from such crosses will not be fixed in subsequent generations, and no selection could be exploited. Modifications to conventional breeding methods could utilize a nonadditive gene effect. On the other hand, low x low could have high sca effects based on dominance x dominance non-allelic interactions, producing over-dominance that could not be fixed and, therefore, cannot be exploited by the standard selection procedure. However, desirable transgressive segregants could be identified in these crosses in later generations with some modifications in conventional breeding methods to capitalize on both additive and non-additive genetic effects (Chakraborty et al., 2009; Verma et al., 2019).

Conclusion

From the present study, it was concluded that the best general combiner for any specific trait might not be the best specific combiner for that trait. There was no single parent and cross, which was superior for all the traits studied. The traits like stem girth, leaf: stem ratio, leaf length, leaf breadth, number of leaves per plant, number of branches per plant, days to flowering, green fodder yield, acid detergent fiber and neutral detergent fiber exhibited additive gene effect. On the other hand, the non-additive gene effect was responsible for the inheritance of traits such as vine length, dry matter yield, crude protein content, and *in-vitro* dry matter digestibility. So, biparental mating in the early segregating generation could be practiced to utilize both additive and non-additive gene action to get desirable segregants for yield and quality in fodder cowpeas.

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